FIREFLY PARASITES AND PREDATORS[1]

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ABSTRACT

Fireflies (Coleoptera; Lampyridae) are parasitized by Diptera (Phoridae, Tachinidae), mites and nematodes. Predator literature is largely anecdotal and speculative—luminescence and chemicals might deter certain predators, and luminescence may attract others. Fireflies are distasteful to some lizards, birds, and mammals. Predators that possibly specialize on fireflies are certain birds (Caprimulgidae, Nyctibiidae), spiders (Lycosidae, Araneidae), certain anoles (Iquanidae) and frogs. Female *Photuris* spp. fireflies are specialized predators of luminescent male fireflies (*Photuris, Photinus, Pyractomena*).

Information on parasites and predators of fireflies is scattered throughout the literature and for the most part is anecdotal. Over the past several years I have collected these notes and anecdotes, reared parasites from fireflies, performed simple predator experiments, and accumulated anecdotes of my own. This paper gathers all of this information and is more historical than scientific; these notes, though interesting reading, unfortunately comprise the substance of scientific knowledge on the subject, a condition which clearly should be corrected. There are a number of reasons why such a compilation may be of value: firefly behavior is important taxonomically and the predators, and perhaps parasites too, have certainly had an influence on the evolution of mating signals and behavior; the literature, as we shall see, is replete with imagined "functions" of firefly luminescence—perhaps this will stimulate some investigation; attempts have been made to use fireflies for biological control (Bess, 1956; Clausen, 1940; Sweetman, 1958)—in a future control program these notes might provide clues to difficulties encountered in trying to understand the behavior and interactions of other species.

PARASITES

Two species of dipterous parasites have been reared from fireflies. A tachinid, *Hyalomyodes triangulifer* (Loew), was reared from *Ellychnia corrusca* (L.) by Sabrosky and Braun (1970), from *Photinus obscurellus* LeC. (D. Oertel, pers. comm.) and I reared it from 3 species in 3 genera (Table 1). I have reared a phorid, *Apocephalus antennatus* Malloch, from 8 firefly species in 3 genera (Table 1). The species parasitized by the phorid are all luminescent as adults. The species parasitized by the tachinid, except *Photinus obscurellus,* are nonluminescent as adults. I found a dipterous (muscoid) maggot partly emerged from under the pronotum of a preserved female *Photinus ignitus* (luminescent species) from Long Island, N. Y. (Fig. 1) which may be a tachinid, but positive identification is not possible.

I observed the emergence of the last 2 of 4 phorids parasitizing a *Photinus macdermotti* female; both emerged from the posterior tip of her abdomen, the third took less than 2 min and the fourth began 1-2 min later and took 45 sec. Of 4 phorids (*Apocephalus* sp.) arrested in the process of leaving a *Pyrac-*

[1]Spiders, fireflies, and parasites are deposited in the Florida State Collection of Arthropods, Gainesville. Some parasitic Diptera are deposited in the USNM, Washington.

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tomena borealis male (and found long after the firefly was pinned) 2 were emerging at the tip of the abdomen, and 2 emerged between the pronotum and the top of the head.

Two phorid adults, *Megaselia* sp., were found in a cage of firefly larvae that had been reared from eggs that were laid in the laboratory by a captive *Photuris* sp. female. Neither their origin, nor the significance of their presence there is known.

Mites are frequently found on firefly larvae and adults: McDermott (1960) noted one on a preserved adult of a *Pyractonema* sp. (not *Pyractomena*) and on living larvae of *Micronaspis floridana* Green (1954). Schwalb (1960) found them on adults and larvae of *Lampyris noctiluca* L. I have found them on adults of *Pyropyga decipiens* (Harris), *Pyropyga minuta* LeC., *Photinus pyralis* (L.), *Photuris lucicrescens* Barber, *Photuris* spp., *Photinus ignitus* (Fig. 2), and others.

Schwalb (1960) reported nematodes in the heads and necks of *Lampyris noctiluca* larvae, and I found them in larval *Pyractomena limbicollis* Green—perhaps ingested with the aquatic snails which I fed them.

Fungi sometimes infect firefly cultures: *Beauveria bassiana* (Bols) (Schwalb, 1960) and *Trichoderma* sp., *Rhyopus* sp., and *Penicillum* sp. (D. Minnick, unpub. ms.).

Predators

Chemical defense: Firefly odors and tastes have been mentioned in the literature on numerous occasions, sometimes specifically in relation to predators: birds don't feed upon *Cratomorphus* sp. "owing to the disagreeable odour, resembling that of phosphorus . . ." (Hudson, 1922); the odor of a firefly made a dog sneeze (Ridley, 1934); "*Luciola* on being crushed emits an unpleasant flavor, but its taste is not at all bitter" (Macloskie, 1885); a crushed *Luciola* sp. "gives out a disagreeable cabbage-like smell, and perhaps this is sufficient to render it inedible to bats or other nocturnal animals. An acrid taste they certainly do not possess" (Packard, 1896); "Between the light which they give and the sticky exudation and unpleasant odour of most species, it seems hardly likely that they would prove a tempting morsel to insectivorous creatures" (McDermott, 1910). Other comments on odor and taste are: a collection of dried *Pyractonema* spp. smelled like *Photinus pyralis* to McDermott (1960); the smell of *Pyractomena borealis* differs from that of *Photinus pyralis* (McDermott, 1917); "I fancied I perceived an odour of the common puff-ball fungus . . ." (Swinton, 1880); a faint musky odor (Ridley, 1934); a peculiar odor (King, 1878); an odor "may be of value in defense, and in making the producing organism unpalatable to its enemies" (Crawford, 1934); "the firefly has a very bitter taste . . ." (S. Watase, see Hearn, 1902); the taste of *P. pyralis* is "slightly astringent but not particularly harsh to a human" (Sexton, 1964); and a nauseating odor when 10,000 - 20,000 are confined in a room (Kiichiro, 1961). I have noticed, with the various species, many of the odors described above, especially the disagreeable cabbage-like odor of the New Guinea firefly *Luciola obsoleta* (Olivier) and the Guadalcanal species *Luciola salomonis limbatipennis* Pic and *Luciola wolfi* Olivier.: some *Photuris* species smell quite plant-like. Many species readily exude fluid from their coxal joints, pronota, and elytra when they are handled roughly; this is

Fig. 1. Muscoid (tachinid?) parasite, now dried and wrinkled from preparation for stereoscan photography, arrested as it emerged from between the head and pronotum of a female *Photinus ignitus* firefly (26X).

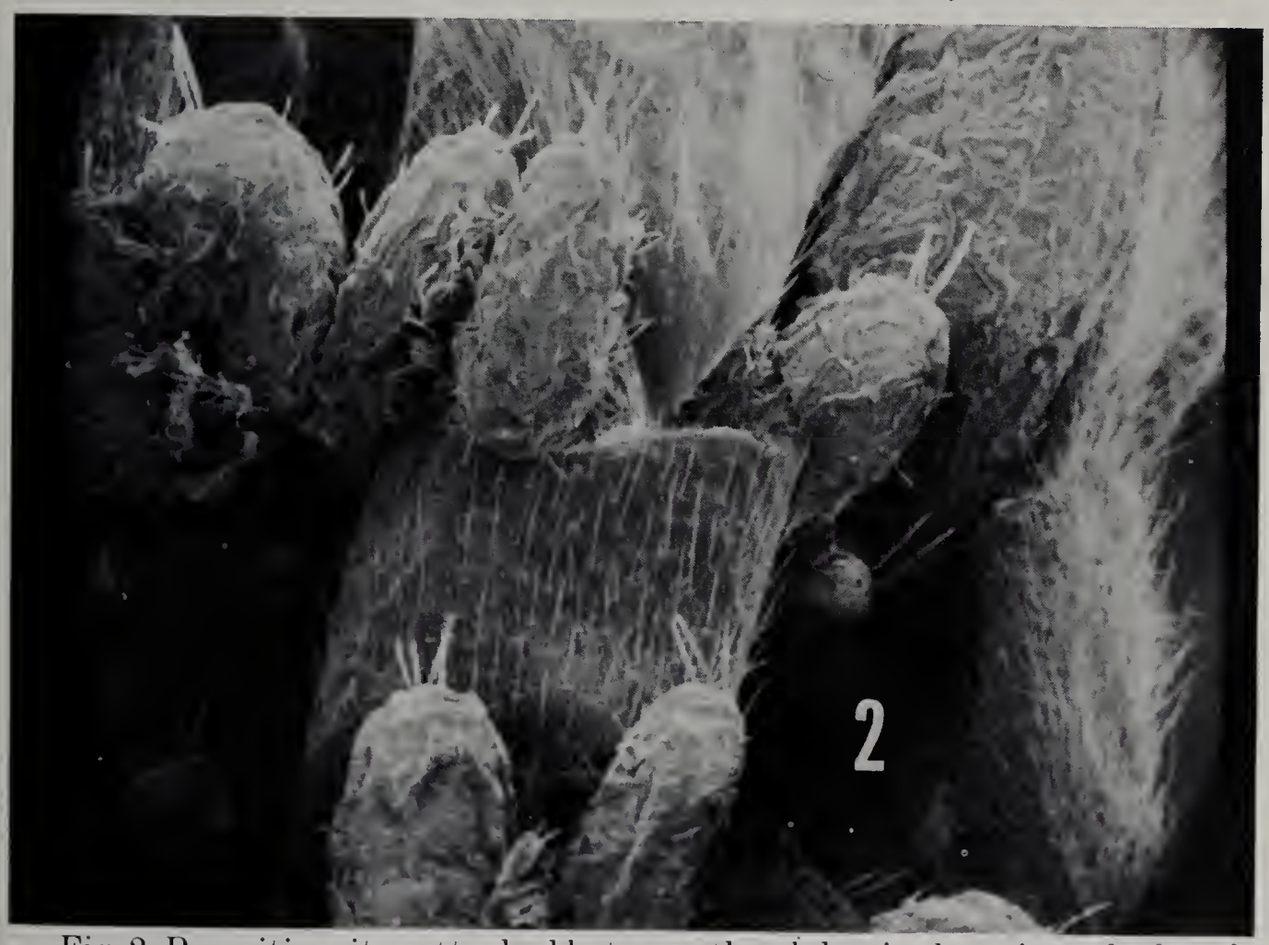

Fig. 2. Parasitic mites attached between the abdominal tergites of a female *P. ignitus* (82X). Eleven mites are visible in this scanning electron micrograph; at least 19 were present.

probably protective (Williams, 1917). W. Kloft (pers. comm.) found that the fluid emitted from a pore in the metathoracic tergite of *Photuris* "D", when the beetle is roughly handled, is haemolymph. He injected radioactive phosphorus into the haemocoel through an intersegmental membrane near the posterior tip of the abdomen. At 7 min. after the injection, radioactivity of the exuded fluid was 4-6 cpm (counts per minute) above background, and at 8 min. it was 185 cpm above background. The rapid appearance of radioactive fluid indicates that the fluid is haemolymph and not a glandular product. Other comments relating to chemical defenses are below.

Luminescent caveat: There have been several suggestions, not necessarily independent, that the luminescence of juvenile and adult fireflies warn predators of the distastefulness of their prospective prey: a toad did not take a glowing firefly offered to it (Schwalb, 1960); "It may also afford the insect a measure of protection for it has been observed that the Carabid beetles leave the fireflies alone" (Guenther, 1931); luminescence possibly warns of inedibility (S. Watase, in Hearn, 1902; Blair, 1915, 1924): "In the case of nocturnal species, the emission of light may serve as a 'warning signal' to bats and nocturnal birds but there is little to support this view" (Maxwell-Lefroy, 1909); "The winged species may also utilize this power to . . . betray their presence to the carnivorous species . . ." (King, 1878); larval lights warn predators (Kaiser, see Harvey, 1952; Hess, 1920; Balduf, 1935); "the flashing light provides . . . a recognition character, so that night-feeding birds and bats avoid attacking these insects" (Dillon, 1967); "May not the light then [if "Lampyridae are distasteful to many insectivora"] serve . . . as a warning of their offensiveness to creatures that would devour them?" (Bowles, 1882); and if the larval bite is poisonous or if fireflies "are disagreeable to the taste the light would of course serve as a danger signal to protect its givers from attack"

TABLE 1. FIREFLY HOSTS OF DIPTERA PARASITES

Dipterous Parasite Firefly Host, Sex	No./Host	Date Left Host	Pupation (days)	Locality
Apocephalus antennatus				
Photuris congener LeC., m	3	27/IV/67	9	Gainesville, Florida
Photuris congener, m	5	4/IV/67	-	Gainesville, Florida
Photuris congener, m	2	3/V/68	15-16	Gainesville, Florida
Photuris sp. *A*, m	2	30/IV/67	22	Gainesville, Florida
Photinus ignitus Fall, f	2	17/VII/64	-	Chenango Forks, New York
Photinus macdermotti Lloyd, f	4	22/VI/68	-	Cockeysville, Maryland
Photinus obscurellus LeC., f	6	15/VI/68	14-15	Oneida, New York
Photinus curtatus X *marginellus,* f	1	21/VII/64	-	Oneida, New York
Photinus consanguineus LeC., m	2	-	-	-
Pyractomena borealis (Randall), m	4	28/III/68	-	Gainesville, Florida
Hyalomyodes triangulifer				
Photinus indictus (LeC.), f	1	15/VII/71	13	Pellston, Michigan
Photinus indictus, f	1	10-12/VII/72	12-14	Pellston, Michigan
Lucidota atra (G. Olivier), f	1	3/VII/71	12-13	Pellston, Michigan
Pyropyga nigricans (Say), f	1	30/VI/71	10+	Pellston, Michigan
Ellychnia corrusca (L.), -	-3-	lab (in lit)	12-13	Beltsville, Maryland
Photinus obscurellus LeC(n=4)	1	4/VII/72	10(n=1)	Woods Hole, Massachusetts

TABLE 2. SPIDER PREDATORS OF FIREFLIES

Firefly Prey, Sex	Spider, Stage, Sex	Locality	Date
Photinus brimleyi, m	*Neoscona arabesca* (Walck.), imm. f	Crailhope, Kentucky	21-VII-63
Photinus brimleyi, m	*Neoscona arabesca*, imm. m	Crailhope, Kentucky	18-VII-63
Photinus brimleyi, m	*Neoscona arabesca*, imm. f	Standing Stone St. Park, Tennessee	5-VII-64
Photinus brimleyi, m	*Neoscona arabesca*, imm. -	Crailhope, Kentucky	8-VII-64
Photinus brimleyi, m	*Verrucosa arenata* (Walck.), imm. f	Crailhope, Kentucky	22-VII-63
Photinus brimleyi, m	*Verrucosa arenata*, sub.ad.f	Crailhope, Kentucky	22-VII-63
Photinus brimleyi, m	*Verrucosa arenata*, ad. f	Crailhope, Kentucky	21-VII-63
Photinus brimleyi, m	*Agelenopsis* sp., imm. f	Crailhope, Kentucky	21-VII-63
Photinus brimleyi, m	*Araneus marmoreus* Clerck, imm. -	Crailhope, Kentucky	22-VII-63
Photinus brimleyi, m	*Eustala anastera* (Walck.), ad. f	Crailhope, Kentucky	22-VII-63
Photinus brimleyi, m	*Micrathena sagittata* (Walck.), ad. f	Crailhope, Kentucky	21-VII-63
Photinus brimleyi, m	*Ummida audouini* (Lucas), ad. f	Standing Stone St. Park, Tennessee	5-VII-64
Photinus collustrans LeC., m	*Acanthepeira venusta* (Banks), ad. f	Gainesville, Florida	5-V-64
Photinus collustrans LeC., m	Lycosidae (not captured)	Gainesville, Florida	19-V-64
Photinus curtatus Green, f	*Neoscona arabesca*, ad. f	Brisban, New York	3-VIII-63
Photinus curtatus X *marginellus*, f	*Neoscona arabesca*, ad. f	Oneida, New York	3-VII-63
Photinus curtatus X *marginellus*, 5 m	*Neoscona arabesca*, ad. f	Oneida, New York	3-VIII-63
Photinus granulatus, m	(ground nesting spider with web over hole)	Wichita, Kansas	27-VI-64
Photinus marginellus, m	*Neoscona arabesca*, ad. f	Greene, New York	21-VII-64
Photinus marginellus, m	*Neoscona arabesca*, ad. f	Chenango Forks, New York	18-VII-64
Photinus marginellus, m	*Neoscona arabesca*, ad. f	Chenango Forks, New York	18-VII-64
Photinus marginellus, m	*Neoscona arabesca*, ad. f	Chenango Forks, New York	18-VII-64
Photinus marginellus, m	*Neoscona arabesca*, ad. f	Greene, New York	22-VII-64
Photinus marginellus, m	*Neoscona arabesca*, ad. f	Greene, New York	18-VII-64
Photinus marginellus, m	*Neoscona arabesca*, ad. f	Ithaca, New York	2-VIII-63
Photinus marginellus, 2m	in web	Chenango Forks, New York	17-VII-64
Photinus obscurellus, m	*Araneus* sp. (probably *cornutus*), imm. f	Oneida, New York	8-VI-64
Photinus pyralis, m	*Neoscona arabesca*, imm. f	Carter Cave, Kentucky	17-VII-63
Photinus pyralis, f	*Enoplognatha marmorata* (Hentz), ad. f	Crailhope, Kentucky	6-VII-64
Photinus pyralis, m	*Acanthepeira stellata* (Walck.), ad. m	Wellington, Kansas	21-VI-64
Photinus sabulosus, m	*Neoscona arabesca*, ad. f	Chenango Forks, New York	17-VII-64
Photinus sabulosus, m	*Neoscona arabesca*, imm. f	Ithaca, New York	2-VII-63
Photinus scintillans, m	*Neoscona arabesca*, imm. f	New Brunswick, New Jersey	7-VII-63
Photinus tenuicincutus, m	*Neoscona arabesca*, imm. f	Fayetteville, Arkansas	30-VI-64
Photuris congener, 4m	seized by lycosid	Gainesville, Florida	14-IV-67
Photuris sp. *A*, m	seized by lycosid	Gainesville, Florida	26-IV-71
Photuris sp., m	*Acanthepeira stellata*, ad. f	Hart Co., Kentucky	17-VII-64
Photuris sp., m	*Neoscona arabesca*, ad. f	Cortland, New York	12-VII-63
Micronaspis floridana Green, f	lycosid	Cedar Key, Florida	12-V-68

(Seaman, 1891). Kirkpatrick (1966: 228), with little data and curious induction, concluded that a defensive function "appears to be the most probable explanation especially since these insects are said to be distasteful." Hudson (1922) thought that the light was not a warning, "That the firefly should have become possessed of so elaborate a machinery, producing incidentally such splendid results, merely as a protection against one set of enemies for a portion only of the period during which they are active, is altogether incredible."

Luminescent bogy: Other workers suggested that the light "frightened," i.e., elicited flight responses in, predators (and others); "the light-producing power . . . [is] for frightening such nocturnal enemies as bats" (Macloskie, 1885); predators are supposed to be frightened by the glowing fireflies that the weaver bird places on its nest (see Harvey, 1952); "*Photuris* larvae were so abundant and so brilliant on the road from Washington to Great Falls as to frighten a pair of spirited horses" (Seaman, 1891); a riding "horse plunged and snorted with alarm" at swarms of fireflies along an Argentinian stream, and raptoral insects are "scared" by firefly light (Hudson, 1922); "three rats on a roof rafter . . . scampered off" (Severn, 1881); a gecko turned and fled from a firefly that flashed (Shelford, 1916; Ridley, 1934); and a chicken fled at the flash of a firefly (McDermott, 1910). When the light of *Phosphaenus hemipterus* Geof. is "not visible a little irritation will render it so. This would make it probable that the light, at least in the male . . . [is used] as a means of frightening its enemies, and warding off danger." This is also probably the case in males of *Lampyris noctiluca* (Jenner, 1883). However, Vogel and Knauer observed that toads, frogs, bats, and spiders are not "frightened" by luminescence (see Schwalb, 1960).

Others have simply noted that fireflies turn on their lanterns when stimulated: *Pyractomena ecostata* (LeC.) adults turn on their light when disturbed (Wenzell, 1896); some larvae shine more brightly if disturbed or "alarmed" (Williams, 1917; Swinton, 1880; McDermott, 1958); adult males of *Pleotomus nigripennis* LeC. glow when disturbed (Sleeper, 1969).

Luminescent target: "While it is supposed by some, that the light of the wingless beetle is bestowed for her protection, to scare away her hungry foes, the nightingale and other birds of night; it is opined by others, that the insect's gift of brilliance . . . is the very mean of her destruction, the very lure and light by which her biped foes are assisted to discover and devour her" (Domestica, 1851:171); "that it is a warning to enemies seems hardly probable, for most small animals, whether aquatic or terrestrial, are attracted rather than repelled by light" (Annandale, 1900); "It guides their enemies—the night hawk and the 'whip-poor-will,' the bat and the owl" (Reid, 1899); "A frog, however, would not be intimidated by their light, which would only draw his attention to his prey" (Guenther, 1931); the light makes larvae and pupae "conspicuous to the eyes of insectivorous birds and other animals" (Seaman, 1891); and larval light "would seem to attract the attention of possible predators such as snakes and skunks" (McDermott, 1958). "Mr. Rennie, by way of disproving Mr. Knapp's theory respecting their dimming their light to escape from birds, positively states that they never extinguish it when alarmed or seized" (Fennell, 1835). "When the nymph is in full glory, she has the power of dimming her lamps, if disturbed by an unwelcome visitor, but can soon rekindle them when her fears are over" (Main, 1834). Aquatic larvae dim their lights when the water is disturbed (Annandale, 1900). "I was told a few days ago of a cat which used to search for and eat glow-worms. It was suggested that she took them for

lights" (Henslow, 1879). "In Jamaica, in some seasons of the year, the fire-flies are seen in the evenings in great abundance. When they settle on the ground, the bull-frog greedily devours them; which seems to have given origin to a curious, though cruel, method of destroying these animals: if red-hot pieces of charcoal be thrown towards them in the dusk of the evening, they leap at them, and hastily swallowing them, are burnt to death" (Darwin, 1791, part II, Canto IV:145). It has been suggested that the flash evolved because the glow attracted predators (Harvey, 1952; Lloyd, 1966). L. Chadwick (pers. comm.) noted that bats on Dominica in the Caribbean dived toward a glowing cigarette each time it was puffed upon and made to glow brightly. Once while I was tape recording the flashes of a firefly female in a glass cage, a frog crashed into the cage; a haiku by Kashi observes, "Drawn by the light of the firefly, swims the frog" (Kiichiro, 1961); the 17th century naturalist John Banister noted, "I have seen our Froggs in an Evening (perhaps mistaking them for fireflies or glow) [Banister's paren, JEL] take in little live coals as greedily as Chickens peck up corn" (Ewan and Ewan, 1970, p. 296).

Other defense: It has also been suggested that the colors and color patterns of fireflies warn predators of unpalatability, that fireflies are involved in mimicry complexes including roaches, soldier beetles, moths, etc. (Belt, 1928; Jones, 1932; McDermott, 1958, 1961; Harvey, 1952, p. 403), and that luminescent elaterid beetles mimic lampyrids and derive protection (A. R. Wallace, see Harvey, 1956). Sexton (1960) manufactured artificial Batesian mimics of *Photinus pyralis* by gluing prothoraces and elytra from these fireflies on adult tenebrionid beetles: "When tested together with unmarked *Photinus,* only the mimics marked with both the prothorax and elytra escape some predation [by the green anole, *Anolis carolinensis*]; when tested together with unmarked *Tenebrio* [*molitor* L.], the mimics marked with elytra as well as those marked with both the elytra and prothorax escape some predation." In another study (1964) he found that "The anoles tended to capture more individuals of unicoloured species of insects than polycoloured species [including *P. pyralis*], whether or not the latter were distasteful or other wise obnoxious". Okada (1928) identified, as defensive organs on *Luciola* larvae, "a row of peculiar forked organs which project outwards further than the gills."

Vertebrate predators: There are several observations of fireflies being eaten or rejected by vertebrates. Monkeys reject fireflies (Belt, 1928), and the bat *Selysius bechsteini* rejected nonglowing fireflies if not mixed with mealworms, and if mixed they would spit them out (Schwalb, 1960). On 2 occasions when I was attracting flying male fireflies to a penlight, bats flew a few feet over my head through what I believed to be the approximate position of the fireflies, and the fireflies did not flash again. In Jahore, West Maylasia, bats attack fireflies that are flying toward (joining) trees with aggregations of fireflies flashing in synchrony (I. Polunin, pers. comm.). When a group of synchronizing fireflies was attracted from a firefly tree to a handheld bar of synchronously-flashing, artificial lights (ca 30 ft. from the tree), bats abruptly moved in and attacked them (F. Hanson, pers. comm.).

Ducks eat firefly larvae along with shellfish (Kiichiro, 1961); fireflies "hide themselves by day; as then their enemies (some of the warblers, it is supposed) are on the alert" (Main, 1834); "my fowls would not touch them" (Belt, 1928); birds rejected *Photuris pennsylvanica*[3] (McDermott, 1958); and on an edibility scale from 00 (inedible) to 100 (completely edible), birds (which

species of the several observed not given) rated *Photinus consanguineus*[3] 00 and *Photuris pennsylvanica*[3] 12.7 (Jones, 1932).

The most interesting note on bird predation is given by Johnson (1937) and concerns the Trinidadian common potoo or poor-me-one, (*Nyctibius griseus*; Nyctibiidae) and fireflies identified as *Elyta* (no such genus known). "I sometimes observed the birds hunting for large fire-flies above the tree-tops in the moonlight. They always did this from a perch, to which they returned like a flycatcher. Since the beginning of April, after dusk the forest was alive with large fireflies (*Elyta*), which set up great dronings in the tree-tops. As 'Poor-me-one' is fond of these insects, it seemed rather that the nesting season would be when they were plentiful, which is in April, May, and June."

Birds of a closely related family (Caprimulgidae) were involved in 2 other interesting observations: "The food of Merrill's Parauque [*Nyctidromus albicollis*], like that of the rest of the Caprimulgidae consists mainly of night-flying insects, such as moths, beetles, etc. The crop of a specimen shot by Mr. H. P. Attwater, near Rockport, Texas, was filled with fireflies, *Photinus pyralis*?" (Bendire, 1895, p. 162). "F. H. Herrick (1901) writes of a Nighthawk [*Chordeiles minor*] that had been feeding on fireflies; the wide open mouth of an adult observed feeding its young was brilliantly illuminated like a spacious apartment all aglow with electricity" (Bent, 1964a, p. 226).

Analyses of bird stomachs have revealed other avian predators: "Fireflies, which are predaceous both in the larval and adult stage, are constantly fed upon by grosbeaks [rose-breasted, *Pheucticus ludovicianus*]. These insects are supposed to be excellent examples of protected species, having the power of secreting nauseous juices, while the 'fire' is supposed to act as a warning signal and certify the bearer's identity to its enemies. It is said that some birds refuse them. However, since 28 rose-breasted grosbeaks [of 176] fed upon them and 6 to 12 of the beetles were found in single stomachs, they must be relished by this species at least" (McAtee, 1908, p 44). McAtee listed 6 species of Lampyridae, 4 of which are now placed in Cantharidae; the remaining 2 species were *Ellychnia corrusca* and *Photinus pyralis*. Beal (1912) examined stomach contents of 100 Acadian flycatchers (*Empidonax virescens*) from 14 states and found *Photinus scintillans*[3] in one; Stoddard (1931) found *Photuris* sp. in one stomach and an unidentified firefly in one stomach (1659 examined) of the Bobwhite (*Colinus virginianus*). Wetmore (1961) examined stomach contents of Puerto Rican birds and found that: 3 Parula warblers (*Parula americana*) had fed upon *Photinus* sp. (*Robopus* sp.) and one upon *Photinus* (now *Robopus*) *vittatus* (61 examined, p 108); one cave swallow (*Petrochelidon fulva*) (of 36, p 87) had eaten *R. vittatus*; one Puerto Rican vireo (*Vireo latimeri*) (of 43, p 96) had eaten *Photinus* sp. (*Robopus* sp.); 3 yellow warblers (*Dendroica petechia*) (of 63, p 106) had eaten *R. vittatus* and 2 had eaten *Photinus* (now *Robopus*) *glaucus* (probably *Robopus dubiosus* (Leng and Mutchler), see Wolcott, 1948); 3 yellow-shouldered blackbirds (*Agelaius xanthomus*) (of 55, p 114) had eaten *R. glaucus* (*R. dubiosus*); and one black-cowled oriole (*Icterus dominicensis*) (of 71, p 116) had eaten *R. glaucus* (*R. dubiosus*).

Other records probably involve soldier beetles (Cantharidae) since they were formerly included in Lampyridae. Such "Lampyridae" were found in the

[3]Species identifications incorrect or doubtful; *P. pennsylvanica* could have been any of several *Photuris* species; *P. consanguineus* probably *P. ignitus*; *P. scintillans* probably *P. marginellus*.

stomachs of: 3 half-grown nestlings of the ovenbird (*Seiurus aurocapillus*) (Judd, 1900, p 416); western bluebirds (*Sialia mexicana*), ruby-crowned kinglets (*Regulus calendula*), and western golden-crowned kinglets (*Regulus satrapa*) (Beal, 1970:18, 100); horned larks (McAtee, 1905:35); 5 Bicknell's thrushes (*Hylocichla minima*) on their breeding ground (Bent, 1964:208); and of robins (*Turdus migratorius*)—"Larvae of the Lampyridae or fireflies, which live in the ground and so fall easy prey to the robin, were found in several stomachs to the extent of upward of a hundred in each" (Beal, 1915:6).

Another study, in which the stomachs of 698 Maryland birds were examined (year 'round, 7 years), found soldier beetles but not fireflies—"Another useful predaceous beetle of the same family, having a similarly repulsive taste, is a firefly, *Photinus*. In June it sometimes, even during daylight, outnumbered the soldier-beetle, [*Chauliognathus pennsylvanicus*] but it was never found in stomachs . . ." (Judd, 1902:37).

Snakes have been suggested as predators of fireflies (Harvey, 1952; McDermott, 1958); Hensoldt (1890) described, in a test of Victorian credulity, the capture of fireflies by a cobra using a glowing stone, the cobra stone, thus "documenting" an Indian legend; Zahl (1962) observed that lizards ate fireflies then spat them out; and a house lizard catching insects on the ceiling would not eat fireflies (Travers, 1924).

In Puerto Rico *Callopisma borencona* Leng and Mutchler is eaten by lizards, *R. vittatus* is eaten by *Anolis cristatellus, R. dubiosus* by *Anolis evermanni* and *Anolis krugii,* and *Robopus roseicollis* Motsch. is "an appreciable item in the food of *A. evermanni* and *A. cristatellus*" (Wolcott, 1948). Sexton (1960) found that *Photinus pyralis* was rejected by the lizards *Anolis carolinensis, Sceloporus undulatus,* and *Eumeces fasciatus,* and 2 species of Venezuelan turtles, *Kinosternon scorpioides* and *Testudo denticulata.* Hungry anoles (i.e., anoles on low rations) are more likely to accept *Photinus pyralis* than lizards on higher rations (Sexton et al, 1966).

I have fed fireflies to 3 species of lizards: the green anole (*A. carolinensis,* 2 specimens), the fence lizard (*S. undulatus,* 4 specimens), and the broad-headed skink (*Eumeces laticeps,* 3 specimens). Fireflies, and the mealworms and crickets used with them, were presented in various ways since the lizards learned and were influenced by repeated test protocols. Prey was dropped into the cages, presented on long forceps, or "under glass" (on a platform while under a clear plastic dish that could be lifted away by a long handle). The latter delayed the lizards' attacks, and they would rapidly circle and poke at the dish, presumably having then a longer period to observe the prey before they could strike.

All lizards rejected *Photinus umbratus* LeC. When seized it was spat out immediately; then the lizard wiped its snout with its forelegs, opened and closed its mouth, and pushed its snout through the sand on the floor of the cage. Similar behavior was observed in *A. carolinensis* by Sexton (1964), in response to *P. pyralis.* Other *Photinus (P. consimilis* complex and *P. consanguineus*) were rejected with similar vigor in the few tests in which they were used. Fireflies frequently survived attack even though seized and roughly spat or thrown several inches. *Photuris* sp. "A" was usually rejected but under certain circumstances (see below) was swallowed.

Fireflies were presented simultaneously "under glass" with mealworms and crickets and with other fireflies of the same and different species. Crickets were also presented with other crickets and mealworms. In these tests the

lizards grabbed the edible species, sometimes quite "delicately" around and over the backs of fireflies. Once, as a mealworm was seized, the antenna of a *Photinus* was also grabbed. The lizard rubbed the firefly away, then rubbed its snout with its forelegs, then swallowed the mealworm. It was in choice tests such as this that *Photuris* fireflies were grabbed and swallowed. On 2 occasions, within seconds of swallowing a cricket, a lizard grabbed and ate the firefly.

Tests performed on lizards, immediately after they were captured, suggested that they had experienced fireflies in nature. A female skink began eating maintenance prey (mealworms, crickets) 4 days after capture but

TABLE 3. FIREFLY PREDATORS OF FIREFLIES

Firefly Predator (females)	Firefly Prey (males)	Source[c]
Photuris jamaicensis Olivier[d]	*Photinus* sp.	Worthy Park, Jamaica T. Walker
Photuris lucicrescens Barber	*Photinus sabulosus* Green	Hancock, Maryland[c]
Photuris pennsylvanica[a]	*Photinus consanguineus*[a]	Hess, 1920
Photuris pennsylvanica[a]	*Photinus marginellus*[a]	Hess, 1920
Photuris pennsylvanica[a]	*Photuris pennsylvanica*[a]	Williams, 1917
Photuris pennsylvanica[a]	*Photinus scintillans*[a]	Williams, 1917; Hess, 1920
Photuris versicolor complex	*Photinus collustrans* LeC.	Gainesville, Florida
Photuris versicolor complex (n = 4)	*Photuris congener*	Gainesville, Florida
Photuris versicolor complex[d]	*Photuris congener*	Gainesville, Florida
Photuris versicolor complex (n = 2)	*Photinus tanytoxus* Lloyd	Gainesville, Florida
Photuris versicolor complex	*Photinus macdermotti*	Lloyd, 1965
Photuris versicolor complex	*Photuris* sp. A.	Gainesville, Florida
Photuris versicolor complex[d]	*Photuris versicolor* complex	Gainesville, Florida
Photuris sp. *A*[b]	*Photinus tanytoxus*	Gainesville, Florida
Photuris sp. *B*	*Photuris* sp. *A*	Gainesville, Florida
Photuris sp. *BR*	*Photuris* sp.	Archbold Biol. Sta., Florida
Photuris sp. *BR*[d]	*Photinus collustrans*	Gainesville, Florida
Photuris sp. *GR*	*Photinus collustrans*	Gainesville, Florida
Photuris sp. *LR*	*Photinus umbratus*	Gainesville, Florida
Photuris sp. *M*	*Photuris* sp. *M*	Pellston, Michigan
Photuris sp. *M*[d]	*Lucidota atra*	Pellston, Michigan
Photuris spp.	*Photinus* spp.	McDermott, 1917; Barber, 1951
Photuris spp.	*Photuris, Photinus, Pyractomena* spp.	Lloyd, 1969
Photuris sp.	*Photinus consanguineus* complex	Fife, Virginia
Photuris sp.	*Photinus floridanus* Fall	Gainesville, Florida
Photuris sp.	*Photuris* sp.	Oneida, New York
Photuris sp.	*Pyractomena angulata* (Say)	Nova Scotia, L. Buschman
Photuris sp.	*Pyractomena borealis*	Nova Scotia, L. Buschman
Photuris sp.	*Pyractomena linearis* complex	Nova Scotia, L. Buschman
Photuris sp.	*Pyractomena linearis* complex	Elizabethville, Ontario, Canada, J. Whitesell
Photuris sp. (n = 2)	*Pyractomena linearis* complex	Ann Arbor, Michigan
Firefly Predators (not adult females)		
Luciola discicollis larvae	*Luciola discicollis* larvae, eggs	Kaufmann, 1965
Photinus larvae[d]	*Photinus* larvae	Gainesville, Florida D. Minnick
Photuris larvae[d]	*Photuris* larvae	Gainesville, Florida D. Minnick, T. Lynch
Pyractomena limbicollis[d] Green larvae	*Pyractomena limbicollis* pupa	Gainesville, Florida

[a]Species determination unreliable. *P. scintillans* = *P. marginellus*.
[b]Species code letters for new and undescribed *Photuris* species now under study.
[c]Locality only indicates J. Lloyd record.
[d]In laboratory.

would not eat fireflies when tested on days 6 and 7. Another skink began eating on day 1 but rejected fireflies when tested for the first time on day 7. A small fence lizard began eating on day 3 and rejected fireflies on day 5. Days or weeks later these same lizards ("had forgotten" and) seized fireflies again. After rejecting fireflies, predators ate maintenance prey. Fourteen (of 22) of Sexton's (1964) anoles would not attack *Photinus pyralis* after an interval of 11 months.

When a firefly was presented to a lizard within a few days of a previous firefly experience it would poke it with its snout and flick its tongue over it, or sometimes, without approaching the firefly, it would "smack its chops" in a fashion similar to that observed after a firefly had been seized (tasted).

Although Schwalb (1960) reported that toads would not take glowing females of *Lampyris noctiluca,* and Sexton (1960, 1964) observed that the Gray Treefrog (*Hyla versicolor*) vigorously rejected *Photinus pyralis*: "The toad advanced toward the beetle, flicked its tongue out and immediately withdrew it after it contacted the beetle. The beetle was left undisturbed in the terrarium side and never entered the hylid's mouth. The final reaction of the toad was to hold its mouth open and partially extend its tongue" (1964:107); other notes on amphibians indicate that they do eat fireflies, and perhaps even hunt them by their luminescence (see above). Harvey (1927) reported a luminous frog from Cuba—it had eaten fireflies, and their lights shone through its belly. I observed a similar event in the Everglades National Park with a green hylid and *Photuris* sp. *A*; Linsenmaier (1972:146) observes, with respect to luminescence 'frightening enemies', "That frogs are unimpressed by it is evident to anyone who sees the curious spectacle of a frog's stomach shining with the light of the firefly larvae it has recently swallowed."; Kiichiro (1961) fed *Luciola* fireflies to a frog and observed light through the frog's belly; "Frogs . . . do not mind the bad taste: they fill their cold bellies with fireflies till the light shines through . . ." (Hearn, 1902, based on S. Watase). A "tamed" luminescing wood frog, *Rang sylvatica,* was photographed for a technical publication dealing with photography, after "it had made a meal of fireflies" (Anon., 1969:50). *Hyla cinerea* eats *Pyractomena lucifera* (Melsh.) (Buschman, pers. comm.); "toads, it is said, have been known to eat them" (McDermott, 1910); and toads eat *Luciola discicollis* Castelnau (Kaufmann, 1965). I fed males of *Photinus umbratus* to 3 toads (*Bufo* sp.). Two of the toads seized and swallowed them, but the third immediately spat out the firefly—and its tongue. The latter hung to the floor for more than a minute while the toad stroked it vigorously with both forefeet. F. Test (pers. comm.) found a living *Pyropyga nigricans* (Say) larva in the stomach of a 40mm leopard frog (*Rana pipiens,* Cheboygan County, Michigan); it had been there at least 24 hours.

Carp eat fireflies in Japanese rice paddies (Kiichiro, 1961), but the aquarium fish *Cichlasoma* sp. rejects *Photinus pyralis* (Sexton, 1960). While working with chemical attraction in *Lucidota atra* at Douglas Lake, Michigan, I placed some females in a boat 20 feet off shore and released males on shore. One male flew out over the water toward the boat and then fell into the water. It was snapped from the surface of the water from below and then reappeared in about 2 seconds.

Invertebrate predators: Spiders are by far the most commonly mentioned invertebrate predators of fireflies (Balduf, 1935; Ridley, 1934; Schwalb, 1960; Zahl, 1962; Shelford, 1916; McDermott, 1958; Wood, 1939); spiders eat

Luciola discicollis (Kaufmann, 1965); *Luciola italica* (L.) is caught in spider webs (Blair, 1915); a salticid captured a *P. lucifera* larva (Buschman, pers. comm.); and although 2 New Guinea fireflies were eaten by the colonial spider, *Cyrtophora moluccensis* (Doleschall), 9 other individuals (*Luciola* spp., *Pteroptyx* sp.) were found under the colonial webs, having been rejected (Y. Lubin, pers. comm.). Table 2 summarizes my data on spiders and their firefly prey.

I once observed a large lycosid that had captured a *P. congener* male. Although the flash code of this firefly is not completely understood, the flash response of the female, and aggressive mimics, to male flashes appears to be rapid single flashes that bear no specific time relationship to the male flashes. The captured male emitted rapid single flashes and drew in 2 more males: the spider grabbed and held these as it ate the first. The sporadic flashes of a *Photuris* sp. "*HS*" male in New York that was dangling in a spider web drew another flying male into the web. I also observed this with a luminescent elaterid beetle, *Pyrophorus texanus* Hyslop, in Texas.

On a number of occasions I have observed lycosid spiders in close proximity to, or capturing perched or grounded, flashing fireflies. While I was attracting a *Photuris* sp. "*A*" male to a flashlight, the firefly was seized by a spider as it walked the last 8 inches to the light, and a *Photinus collustrans* LeC. male that was walking to a glowing female in an open dish (in which I had placed her to attract a male) was seized by a lycosid that dashed away with him several inches before dropping him. Males of *Photinus umbratus* remain perched on low grass flashing after their evening activity: several times I have found lycosids within inches of them or eating them.

Other invertebrates reported to have eaten fireflies are a snail (ate a glowworm) (Newall, 1897), a brown centipede (McDermott, 1958), the Monedula wasp and an asilid fly (Hudson, 1922), a crustacean (*Cambaroides japonicus*) (Kiichiro, 1961), and a staphilinid beetle (*Goerius,* now *Staphilinus olens*) (Dale, 1834). The pupa of a firefly I was rearing (*Pyractomena dispersa* Green) was eaten by a pillbug *Armadillidium* sp., and on 3 occasions I have seen harvestmen eating living fireflies (*Photuris* spp., *P. scintillans*). In one situation the firefly was flashing brightly, and it was well after dark. One harvestman has been identified as *Leiobunum* sp.

The fire ants, *Solenopsis geminata* (Fabr.) and *S. invicta* Buren, ate *Photuris* sp. fireflies placed in a test chamber attached to their nest by a glass tube, but *Conomyrmex pyramicus* (yellow form) did not, although it did take other insects (A. Bhatkar, pers. comm.). Black ants in West Africa eat *Luciola discicollis* (Kaufmann, 1965), *Oecophylla* sp. in Jahore feeds upon *Pteroptyx* fireflies (I. Polunin, pers. comm.), *Solenopsis molesta* (Say) ate dead *P. pennsylvanica*[3] and *P. consanguineus*[3] (Jones, 1932), and ants ate 6 non-luminescing fireflies but left glowing ones untouched (Travers, 1924). I fed *Photinus obscurellus* to antlions, and in the field found a reduviid bug (*Zelus* sp.) feeding upon a female *Photuris congener*. F. Hanson (pers. comm.) in Hoskins, New Britain, observed the attack of a reduviid bug upon a male *Pteroptyx* firefly: the firefly was seized and quickly released, apparently unharmed. I fed several fireflies to the mantid *Brunneria borealis* Scudder. It ate *Photuris* sp. "*A*" and rejected *Photinus umbratus* several times. It accepted a *Photinus consanguineus* male, chewed on him several seconds then dropped him. It rejected this firefly once again after eating a mealworm. After eating a second mealworm it ate the firefly. Linn (1972) "watched a pet praying mantis repeatedly seize fireflies tentatively and then throw them as far away as possible."

Firefly females of some *Photuris* species are carnivorous. Furthermore, some mimic the mating flashes of females of other species, attract their males, and eat them (Lloyd, 1965, 1969). There are several literature accounts of *Photuris* sp. females eating males of other species. Table 3 lists these, along with personal communications, and my own records.

Other suggested functions of firefly luminescence pertaining to predator defense are protective resemblance to luminescent bacteria and fungi (Lloyd, 1966, p 68), and dazzling the eyes of predators and disguising the insect's position (Riley, 1880). It is only a matter of time until a theoretical ecovitalist suggests that luminescence is part of a "homeostatic mechanism" to regulate population density by attracting predators to eat up superfluous individuals for the good of the species.

In conclusion, actual knowledge of firefly predators is meager, but it suggests that (some) fireflies are distasteful to some predators, and that some predators such as goatsuckers (Caprimulgidae), potoos (Nyctibiidae), spiders (Araneidae, Lycosidae), certain anoles (Iguanidae) and frogs possibly specialize on firefly prey at least during certain times or seasons. Other records of vertebrate predation appear to be incidental. Firefly females of several *Photuris* species prey upon the males of several species of *Photinus, Photuris* and *Pyractomena.*

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BOOK REVIEW

Bibliography of Interlingual Scientific and Technical Dictionaries (Fifth Edition). 1969. Unipub, Inc., P.O. Box 433, N.Y., N.Y. 10016. 250 p. Cloth, $9.00.

This is an unusual bibliography since it covers 2,491 dictionaries under 263 subject headings and 75 languages. Over 200 entries are cross-referenced, and there is an index to author, subject, and language. There are only 16 dictionaries listed under zoology and 1 under "Insectology", although a variety of other entries would also be of interest to biologists. A great time-saver in locating such dictionaries.—R. E. Woodruff.